



Research Article

Distance From Riparian Edge Reduces Brood Parasitism of Southwestern Willow Flycatchers, Whereas Parasitism Increases Nest Predation Risk

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ABSTRACT The southwestern willow flycatcher (*Empidonax traillii extimus*) is a federally endangered subspecies that breeds in increasingly fragmented and threatened habitat. We examined whether temporal and habitat characteristics were associated with risk of predation and probability of brood parasitism by brown-headed cowbirds (*Molothrus ater*) on flycatcher nests at 6 sites in southern Nevada and northwestern Arizona, USA. For nest predation, we found the most support for a model that included date and an interaction between parasitism status and nesting stage. Daily nest survival decreased from 0.87 (95% CI = 0.81–0.93) to 0.78 (95% CI = 0.72–0.84) through the season for parasitized nests but remained relatively constant for unparasitized nests (0.93, 95% CI = 0.91–0.95 to 0.92, 95% CI = 0.91–0.93). Parasitized nests had lower survival than non-parasitized nests during the incubation (0.85, 95% CI = 0.84–0.86 vs. 0.92, CI = 0.91–0.93) and nestling (0.79, 95% CI = 0.77–0.81 vs. 0.91, 95% CI = 0.90–0.92) stages. Of the variables included in our parasitism candidate models, model-averaged coefficients and odds ratios supported only distance to habitat edge; odds of parasitism decreased 1% for every 1 m from the habitat edge. Nests greater than 100 m from an edge were 50% less likely to be parasitized as those on an edge, however, only 52 of 233 nests (22%) were found at this distance. Where management and conservation goals include reducing nest losses due to parasitism, we recommend restoration of habitat patches that minimize edge and maximize breeding habitat further from edges. At sites where cowbirds have been documented as important nest predators, controlling cowbirds may be one option, but further study of the link between parasitism and nest predation and the identification of major nest predators at specific sites is warranted. © 2011 The Wildlife Society.

KEY WORDS brown-headed cowbird, *Empidonax traillii extimus*, habitat, lower Colorado River, *Molothrus ater*, nest predation, southwestern willow flycatcher.

Recovery of threatened and endangered populations requires an understanding of the factors limiting productivity and survival. For North American passerine birds, brood parasitism by brown-headed cowbirds (*Molothrus ater*; hereafter cowbirds) and nest predation are the 2 main causes of nest failure (Martin 1992, Schmidt and Whelan 1999) and both can negatively affect reproductive success and potentially contribute to population declines (Brittingham and Temple 1983, Heske et al. 2001). Although the percentage of nests lost to nest predation is often higher than the percentage parasitized, parasitism has been considered

an important additive factor limiting reproductive success in small populations of some endangered birds (e.g., DeCapita 2000, Griffith and Griffith 2000, Ward and Smith 2000). The southwestern willow flycatcher (*Empidonax traillii extimus*; hereafter flycatcher) is a small-bodied, generalist insectivore representative of many open-cup nesting Neotropical migrants breeding in remnant patches of southwestern riparian habitat. This subspecies is protected under the Endangered Species Act (U.S. Fish and Wildlife Service [USFWS] 1995) due to historical reductions in population size and has been the focus of major monitoring and management efforts. Most populations are small, consisting of fewer than 5 pairs (Sogge et al. 2003). Reduction in population size has been attributed primarily to riparian habitat loss, fragmentation, and modification (USFWS 1995). Brood parasitism, though variable across the flycatcher's range, may contribute significantly to reduced reproductive success

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(e.g., Sedgwick and Iko 1999, Uyehara and Whitfield 2000, Brodhead et al. 2007). Reproductive losses to nest predation are generally much higher than those to parasitism (Sedgwick and Iko 1999, McLeod et al. 2008) and documented nest predators include several species of hawks, owls, snakes, passerine birds, and skunks (L. Ellis, Arizona Game and Fish Department, personal communication; T. Theimer, Northern Arizona University, unpublished data).

Numerous studies have examined habitat features correlated with either predation or parasitism (e.g., Ward and Smith 2000, Davidson and Knight 2001, Stoleson and Finch 2001), but fewer studies have evaluated predation and parasitism in the same system (exceptions include Larison et al. 1998, Parker 1999, Budnik et al. 2002, Cain et al. 2003). Spatially variable rates of predation and parasitism suggest that habitat characteristics may play an important role in determining predation and parasitism risk (Burhans et al. 2002, Thompson et al. 2002). Therefore, identifying habitat characteristics associated with nest predation and parasitism is an important first step in determining whether habitat modification could be a feasible and cost-effective method to reduce either factor, as suggested by Robinson et al. (2000), and thereby increase the probability of persistence of endangered passerine populations. Separating the effects of predation and parasitism may be difficult, however, because cowbirds may act as predators (Granfors et al. 2001, Stake and Cimprich 2003, Hoover and Robinson 2007, Benson et al. 2010) and parasitized nests may share habitat characteristics with depredated nests (Arcese et al. 1996). In spite of these challenges, understanding the factors that affect nest predation and brood parasitism is critical for managers faced with maintaining declining populations of songbirds in increasingly human-altered landscapes like those of the riparian forests of the American southwest (Rich et al. 2004).

Our primary goals were to determine whether temporal, edge, or habitat characteristics at and around flycatcher nests were associated with the likelihood of nest predation or parasitism and whether these 2 major effects on nest survival were influenced by similar factors. Our secondary goal was to assess whether the same management approaches could reduce the effect of both nest predation and nest parasitism on this endangered bird.

STUDY AREA

We monitored flycatcher nests at 6 sites along the lower Colorado River (LCR) in Arizona and the Virgin River in Nevada (Fig. 1) from 2003 to 2007. These sites represent all known flycatcher breeding habitats along the LCR and its nearby tributaries. Mesquite (hereafter MESQ; 36°48'08" N, 114°3'53" W) lies along the Virgin River and consists of a relatively equal mix of tamarisk (*Tamarix* spp.) and Goodding's and coyote willow (*Salix gooddingii* and *S. exigua*) and encompasses 42 ha of land, approximately 5 ha occupied by breeding flycatchers. Mormon Mesa (hereafter MOME; 36°30'38" N, 114°22'27" W), also on the Virgin River, consists mainly of tamarisk, although flycatcher breeding areas are located in patches of Goodding's and coyote willow and includes 125 ha of land, though only

10 ha were used by breeding flycatchers. The Overton Wildlife Management Area (hereafter MUDD; 36°33'48" N, 114°20'40" W) is located along the Muddy River and consists mostly of tamarisk, with a small section of Goodding's willow in the southern portion of the site covering 16 ha, with breeding flycatchers using approximately 1 ha. The Grand Canyon site (hereafter GRCA; 35°47'11" N, 113°30'44" W) is comprised of many small, isolated patches of tamarisk, Goodding's willow, and coyote willow in lower Grand Canyon and Lake Mead National Recreational Area totaling 121 ha, though breeding pairs used less than 5 ha. Topock Marsh (hereafter TOPO; 34°43'25" N, 114°26'09" W) is located in the Havasu National Wildlife Refuge and is an extensive stand of tamarisk bordering a large marsh with small, isolated patches of emergent Goodding's willow spanning 65 ha, though breeding was limited to approximately 35 ha. The Bill Williams River National Wildlife Refuge (hereafter BIWI; 34°18'33" N, 114°1'30" W) is the southernmost known breeding location for flycatchers on the LCR. It contains the largest contiguous stand of native (Goodding's willow) riparian vegetation along the Colorado River with an understory of tamarisk, covering 86 ha, with breeding flycatchers using only 17 ha.

METHODS

Nest Monitoring

We located and monitored flycatcher territories and active nests using a modification of the Breeding Bird Research and Monitoring Database (BBIRD) protocol (Martin et al. 1997) from May through August 2003–2007. We monitored active nests using a mirror pole every 2–4 days until nestlings were 8 days old, after which we assessed nest fate until failure or fledging (at approx. 12 days) by observing the nest from the ground to reduce the risk of force fledging. We recorded nest stage based on contents of the nest when we were able to directly see into the nest and based on female behavior (e.g., brooding eggs or feeding nestlings). We made every attempt to monitor the nest on transition days, but if we were not able to, the stage transition date was estimated as the day midway between the 2 monitoring intervals.

We recorded nest height, canopy height (mean height of canopy within an 11.3-m radius from the nest), ground cover (mean percentage of woody debris within 1-m squares placed 1 m from the nest in each cardinal direction), and canopy cover (average of 2 densiometer readings taken at 1 m north and 1 m south of the nest) for each nest. We measured vegetation at the end of the nesting season to minimize disturbance during the nesting period, an approach used in other studies (Parker 1999, Cain et al. 2003, Brodhead et al. 2007, Kus et al. 2008, Benson et al. 2010) and of special concern when working with endangered species. Although measurement lag (elapsed time between lay date and measurement of vegetation) potentially confounds comparison of vegetation characteristics at early versus late nests, the only study to test this directly found that measurement lag explained only 4–6% of the variation in riparian habitat



Figure 1. Location of the 6 study sites where we monitored southwestern willow flycatcher nest fate from 2003 to 2007.

variables (Sharp and Kus 2006). We measured distance to habitat edge by plotting nest locations in a Geographic Information System (GIS) framework onto high-resolution aerial photographs at the end of the breeding season. We defined a habitat edge as a major shift in the dominant vegetation or habitat (e.g., from riparian habitat to agriculture, road, field, upland desert vegetation, river, or marsh) with a canopy opening ≥ 10 m.

Analysis

We focused on factors associated with nest predation and parasitism; therefore, we excluded all nests that we knew failed due to weather or female abandonment (12 nests). We

also excluded all nests where parasitism coincided with egg predation (i.e., when a flycatcher egg was missing during the same interval that a cowbird egg appeared) to reduce the confounding effects of cowbirds acting as egg predators. For each monitoring interval, nests were categorized as 1) partially depredated when only some of the eggs or nestlings present were depredated, 2) fully depredated when all eggs or nestlings were depredated, 3) parasitized when the nest contained at least 1 cowbird egg, and 4) successful if the nest fledged at least 1 flycatcher young.

We used an information-theoretic approach (Akaike's Information Criterion corrected for small sample sizes [AIC_c]; Burnham and Anderson 2002) to determine support

for temporal and habitat models that represented a priori hypotheses about factors that affect probability of predation and/or parasitism events (regardless of eventual nesting outcome). Predation and parasitism pressure may vary with time (Stake and Cimprich 2003, Peak 2007, Reidy et al. 2009), so we first evaluated support for temporal models using 3 temporal covariates that varied over time, nesting stage (laying, incubation, nestling), date (median ordinal date of interval), and year (of nesting attempt), and all combinations of these variables (Grant et al. 2005, Reidy et al. 2009). We then included the temporal factors that appeared in the most supported models (those with $\Delta AIC_c \leq 2$; Burnham and Anderson 2002) in all of our subsequent habitat models (Grant et al. 2005, Reidy et al. 2009).

We performed separate analyses to examine the effects of habitat characteristics on predation and parasitism. To assess factors associated with nest predation, we evaluated relative support for 14 a priori models (see Table S1, available online at www.onlinelibrary.wiley.com) that related nest predation to 1) parasitism status of the nest (a static covariate), 2) an interaction between parasitism status and nest stage, 3) site, and 4) the individual and combined effects of each of the habitat characteristics described above. We also combined habitat variables into 3 additional models based on a priori assumptions of how they may affect predator behavior: 1) a visual detection model that predicted predators' ability to find nests would be influenced by canopy cover, ground cover, and nest height, 2) a ground access model that predicted ground predators would be influenced by nest height, ground cover, and distance to edge, and 3) an aerial access model that predicted aerial predators would be influenced by canopy cover and distance to edge. Lastly, we included a global (all covariates) model, a temporal model (using the most-supported temporal covariates from the first stage of analysis), and a null (intercept only) model. To assess factors associated with parasitism we again compared null and global models to those including site and to models containing individual and combined effects of habitat variables for a total of 12 models (see Table S1, available online at www.onlinelibrary.wiley.com). We combined habitat variables into 2 models based on how factors potentially influenced cowbird parasitism: 1) a visual search model that predicted cowbirds' ability to find nests visually was influenced by nest height, ground cover, canopy cover, and canopy height and 2) a cowbird nest access model that included canopy cover and distance to edge.

We evaluated support for candidate models in each suite using AIC_c and AIC weights (w_i ; the relative likelihood that the model is the best model, given the model set; Burnham and Anderson 2002). We used effective sample size to compute AIC_c (Rotella et al. 2004; n = number of successful nest days + number of intervals in which a predation event occurred) for predation models. For both predation and parasitism analyses, models with a $\Delta AIC_c \leq 2.0$ were considered to have the most support (Burnham and Anderson 2002) and we report results of the 90% confidence set of models (Burnham and Anderson 2002). When no single model was most strongly supported by the data, we

report model-averaged parameter estimates (β), unconditional standard errors (SE), odds ratios, and 95% confidence intervals for each covariate based on a >90% confidence set of models to guard against potential effects of model uncertainty (Burnham and Anderson 2002). Model averages were computed using all models and the value of the coefficient was treated as zero in cases where the variable did not occur in a given model (Burnham and Anderson 2002).

For our analysis of predation, we fit each model using Shaffer's (2004) logistic exposure method. This method, analogous to the Mayfield method (Mayfield 1961, 1975), incorporates the number of exposure days to account for nests that were never observed or were not checked daily. This approach allowed us to include temporal factors (year, date, and stage) that potentially varied among intervals. We modeled daily survival rate (DSR; Shaffer 2004) for predation analyses using a binomial response (success = 1, predation = 0) and the logit link function outlined in Shaffer (2004). However, because parasitism occurs within a relatively short interval during the laying and early incubation stages, we fit parasitism models using a standard logistic regression approach (Agresti 2002, Sharp and Kus 2006) again using a binomial response (parasitized nests = 1, non-parasitized nests = 0) using the standard logit link function (Agresti 2002).

For both sets of analyses, we examined the global model for each set of models for evidence of lack of fit (Burnham and Anderson 2002). We fit models in R (Version 2.9.1, 2009). We estimated daily survival rates and probability of parasitism as a function of the variables of interest (we held continuous variables constant at their mean values and categorical variables at values corresponding to the proportions in which they were observed in each category; Shaffer and Thompson 2007) using the 90% candidate set of models (Burnham and Anderson 2002).

Different types of predators may be associated with complete versus partial predation events (Robinson and Robinson 2001, Small et al. 2007), so we carried out the analyses described above 3 times, first using only partial predation events as our response variable, second using only complete predation events, and last using all predation events. We examined support for the same suite of candidate models used in our predation analysis using the logistic exposure method (Shaffer 2004) in all 3 cases.

RESULTS

From 2003 to 2007, we monitored 233 flycatcher nests (37 in 2003, 52 in 2004, 51 in 2005, 50 in 2006, and 43 in 2007) that resulted in 1,740 monitoring intervals used for our predation analysis (effective sample size = 4,037; Rotella et al. 2004). We recorded 165 predation events (70.8% of all nests) with 88 partial and 77 full predation events. Levels of predation varied across sites, ranging from 38.5% at BIWI to 78.9% at MUDD (Table 1). We documented parasitism at 62 nests (22.6% of all nests) and 26 (41.9%) of these nests were also depredated. Parasitism rates ranged from 0% at GRCA to 31.6% at MUDD (Table 1). Mean interval length (time between nest checks) was 2.5 days.

Table 1. Percentage of southwestern willow flycatcher nests depredated and parasitized (and total number of nests) at each of 6 sites in western Arizona and southern Nevada, USA, 2003–2007.

Site	No. nests	No. depredated (%)	No. parasitized (%)
Bill Williams NWR, AZ	13	5 (38.5)	2 (15.4)
Grand Canyon	4	3 (75.0)	0 (0.0)
Mesquite, NV	75	52 (69.3)	18 (24.0)
Mormon Mesa, NV	33	24 (72.7)	4 (12.1)
Muddy River, NV	19	15 (78.9)	6 (31.6)
Havasu NWR, AZ	89	67 (75.3)	21 (23.6)

Predation

The results of analyses based on only partial predation events, only complete predation events, and on total predation events did not differ, so we report here only the results based on all predation events combined. Although some of the partial depredation events we documented could have been due to nestling starvation, most of these events occurred at the egg stage. The 2 most supported models in the first stage of the analysis included nest stage and date models ($w_i = 0.49$ and 0.31 , respectively). We therefore included stage and date in all habitat models. Of the 14 predation models, only 1 model, which included the temporal variables and an interaction between parasitism status and nest stage, had a $\Delta AIC_c \leq 2.0$ (Table 2a). Our global model did not indicate a lack of fit or exhibit evidence of overdispersion ($\hat{c} = 0.63$). We did not model average any of the parameters for our predation analysis because the top model accounted for 93% of the total weight among the candidate models and all other models were less supported by the data ($\Delta AIC_c > 5.25$). Using the best-supported model for prediction, daily nest survival decreased from 0.87 (95% CI = 0.81–0.93) to 0.78 (95% CI = 0.72–0.84) throughout the season for parasitized nests when averaged across all stages. For unparasitized nests, daily nest survival remained relatively constant throughout the season (0.93, 95%

CI = 0.91–0.95 to 0.92, 95% CI = 0.91–0.93) and was relatively constant across laying, incubation, and nestling stages. Daily survival of parasitized nests was similar to that for unparasitized nests at the laying stage (0.93, 95% CI = 0.92–0.94 vs. 0.94, 95% CI = 0.93–0.95) but was lower during the incubation stage (0.85, 95% CI = 0.84–0.86 vs. 0.92, CI = 0.91–0.93) and lower still during the nestling stage (0.79, 95% CI = 0.77–0.81 vs. 0.91, 95% CI = 0.90–0.92). This pattern across nest stages was reflected in a decrease in daily nest survival through the season for parasitized nests during the incubation and laying stages and an overall lower nest survival for parasitized nests during the nestling phase (Fig. 2). Mean habitat variables were similar for nests that experienced predation compared to those that did not (Table 3) and coefficients for all variables except stage and parasitism status in the global model were close to zero, suggesting that parasitism status and stage were the most important for predicting predation.

Parasitism

The most supported models in the first stage of our parasitism analysis included ordinal date and year (of nesting attempt), a model with only ordinal date, and a model with only year ($w_i = 0.37$, 0.32 , and 0.18 , respectively); therefore, we included ordinal date and year in all habitat models. The global model did not reveal significant lack of fit ($\hat{c} = 1.0$). Only 2 parasitism models had $\Delta AIC_c \leq 2.0$ (Table 2b) and all other models were less supported by the data ($\Delta AIC_c > 4.25$, Table 2b). The 2 best-supported models included a model with temporal variables and distance to edge and a model with temporal variables, canopy cover, and distance to edge ($w_i = 0.44$ and 0.35 , respectively, Table 2b). However, 5 models were part of the >90% confidence set of models and included temporal variables (ordinal date and year), distance to edge, canopy cover, and nest height.

Distance to edge was most strongly associated with parasitism, and it occurred in 2 of the models in our candidate set

Table 2. Statistics for the 90% confidence set of models used to predict (a) predation (effective $n = 4,037$) and (b) parasitism ($n = 233$) of southwestern willow flycatcher nests at 6 sites in western Arizona and southern Nevada, USA, 2003–2007.

	K^a	AIC_c^b	ΔAIC_c^c	w_i^d	Residual deviance
(a) Predation models					
Temporal ^e + parasitism status \times stage	9	1,328.82	0	0.93	1,310.8
Temporal ^e	5	1,360.67	26.56	0	1,350.7
Intercept only	1	1,363.96	29.85	0	1,362.0
(b) Parasitism models					
Temporal ^f + distance to edge	7	282.93	0	0.44	282.4
Temporal ^f + canopy cover + distance to edge	8	283.34	0.42	0.35	282.7
Temporal ^f	6	287.14	4.22	0.05	274.8
Temporal ^f + canopy cover	7	287.62	4.69	0.05	287.1
Temporal ^f + nest height	7	287.97	5.05	0.03	287.5
Intercept only	1	289.39	6.46	0.02	289.4

^a Number of parameters.

^b Akaike's Information Criterion values, corrected for small sample size.

^c Difference between AIC_c value of current model and most-supported model.

^d Relative likelihood that the model is the best model.

^e Nest stage and ordinal date.

^f Ordinal date and year.

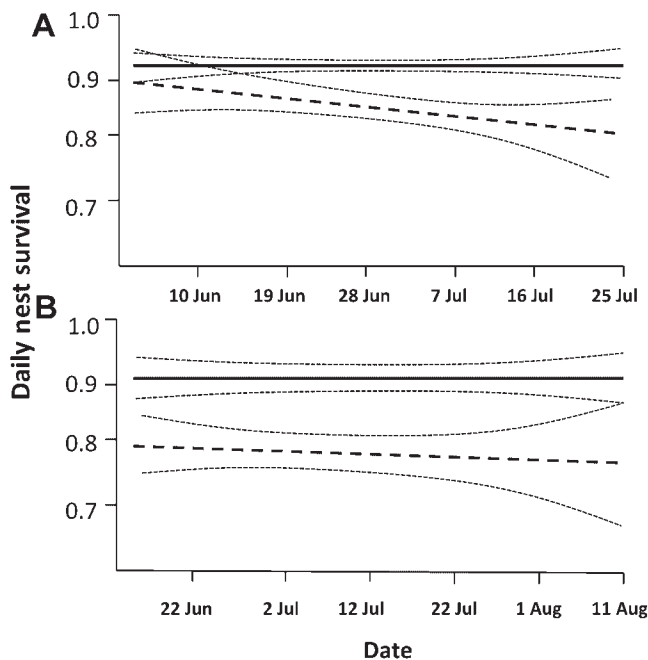


Figure 2. Estimated daily nest survival and 95% confidence intervals during (A) laying and incubation and (B) nestling stages of parasitized (dashed lines) and unparasitized (solid lines) nests of southwestern willow flycatchers in Arizona and Nevada, USA, 2003–2007.

(Table 4). The model-averaged parameter estimates indicated a negative relationship between probability of parasitism and distance from edge (Table 4, Fig. 3) and the 95% confidence interval of the odds ratio did not overlap 1 (Table 4). The odds of parasitism were 1% less for every 1 m from the habitat edge (Table 4). Odds ratio 95% confidence intervals from model-averaged regression coefficients for canopy cover, nest height, ordinal date, and year all overlapped 1 (Table 4) and mean, median and range of these parameters were similar for most (Table 3), making it difficult to assess the strength of these effects. However, although mean day of nest initiation did not differ between parasitized

and unparasitized nests, median date was 1 week later for parasitized nests (Table 3) reflecting an overall pattern of lower parasitism rates earlier in the season.

DISCUSSION

Distance to edge was not associated with predation in our study but nests that were closer to an edge were more likely to be parasitized. A decline in parasitism with distance from edge is consistent with many studies (e.g., De Santo and Willson 2001, Bakermans and Rodewald 2006, Brodhead et al. 2007) and contrasts with others (e.g., Hahn and Hatfield 1995, Burhans and Thompson 1999). We found that nests greater than 100 m from an edge were 50% less likely to be parasitized as those on an edge, however, only 52 of 233 nests (22%) were found at this distance. Most of our study sites were small, however, and there was little habitat available to flycatchers greater than 100 m from an edge. Investigating the relationship between parasitism and distance from edge at distances greater than 100 m for southwestern willow flycatchers would require studying these effects at sites large enough to allow nests to be placed farther from an edge, but few occupied sites are currently that large. The dependence of parasitism on distance from edge, and the fact that parasitized nests suffered higher predation rates, suggests that nest predation also should have been associated with distance from edge. We believe we failed to find an edge effect for nest predation because there were more nests that suffered predation than were parasitized, and overall nest predation was not strongly associated with distance from edge in our system. Higher nest predation along edges is typically attributed to higher predator activity (Cain et al. 2003) and abundance (Gates and Gysel 1978, Donovan et al. 1997) near edges. Failure to find an edge effect on predation, as in our study, could be due to either a suite of nest predators less sensitive to edge (e.g., Morrison and Bolger 2008) or to a diverse predator guild that varies in its sensitivity to edge (Thompson and Burhans 2003, Benson et al. 2010). Further work to elucidate the predator community at our sites is needed to clarify which of these is more likely.

Table 3. Descriptive statistics for covariates used to predict predation and parasitism of southwestern willow flycatcher nests at 6 sites in Nevada and Arizona, USA, 2003–2007

Nest fate	Statistic	Initiation date	Distance from edge (m)	Nest ht (m)	Canopy ht (m)	Ground cover (%)	Canopy cover (%)
Depredated (<i>n</i> = 165)	Mean	20-Jun	65.2	2.9	6.4	18	92.9
	SE	1.3	5.9	0.1	0.2	1.6	0.6
	Median	20-Jun	45	2.6	6	11.8	94.8
	Range	22 May–23 Jul	5–350	1–6.7	3–17.6	0–85	59–100
Surviving (<i>n</i> = 68)	Mean	20-Jun	61.9	3	6.5	17.7	92.9
	SE	1.2	6	0.1	0.2	1.8	0.7
	Median	16-Jun	40	2.7	6.2	12	95
	Range	27 May–16 Jul	5–250	1–6.5	2.8–13	0–100	54–100
Parasitized (<i>n</i> = 62)	Mean	23-Jun	45.5	2.8	6.2	18.2	91.9
	SE	1.8	6.4	0.1	0.2	2.3	1.1
	Median	22-Jun	30	2.7	6	13	94.8
	Range	28 May–20 Jul	5–250	1–5.2	3.5–11.5	0–72	59–100
Not parasitized (<i>n</i> = 171)	Mean	20-Jun	65.7	2.9	6.4	16.9	96.9
	SE	1	5.2	0.1	0.1	1.3	0.2
	Median	16-Jun	45	2.6	6.1	11	94.9
	Range	22 May–20 Jul	5–350	1–6.7	2.8–17.6	0–100	54–100

Table 4. Model-averaged coefficients and odds ratios from models predicting parasitism of southwestern willow flycatcher nests at 6 sites in western Arizona and southern Nevada from 2003 to 2007.

Variable	β (Var) ^a	Odds ratio (CI)
Distance to edge	−0.007 (0.003)	0.993 (0.987, 0.999)
Canopy cover	0.005 (0.021)	1.005 (0.995, 1.016)
Nest height	−0.032 (0.003)	0.968 (0.906, 1.031)
Date	0.019 (0.011)	1.019 (0.997, 1.041)
Year (2003 vs. 2004)	0.829 (0.544)	2.509 (0.948, 4.070)
Year (2003 vs. 2005)	0.829 (0.555)	2.509 (0.884, 4.13)
Year (2003 vs. 2006)	−0.142 (0.598)	0.845 (0.329, 2.038)
Year (2003 vs. 2007)	0.401 (0.601)	1.560 (0.248, 2.852)

^a Model-averaged regression coefficients (β) and unconditional variance estimates (Var).

None of the other habitat characteristics we examined were strongly associated with either predation or parasitism, although they have been implicated in previous studies. Canopy cover has been negatively associated with parasitism (e.g., Burhans 1997, Averill 1998, Uyehara and Whitfield 2000), however, because flycatchers preferentially nest in sites with high canopy cover (McLeod et al. 2008), our ability to detect an effect of canopy cover on parasitism and predation may have been more limited in this study than in those studying passerines that nest over a broader range of canopy cover values. Likewise, although a previous study of flycatchers along the Gila River in New Mexico found that parasitism was lower at lower nest heights (Brodhead et al. 2007), we found little support for an association between nest height and parasitism. This may have been because mean nest height in our study was relatively low and less variable (Table 3) than nest heights reported in Brodhead et al. (2007; e.g., parasitized and unparasitized nest heights along the Gila River were 4.7 m and 6.8 m, respectively). Finally, habitat features we did not measure, such as foliage density immediately surrounding the nest, may be more important for aerial predators and cowbirds (Parker 1999).

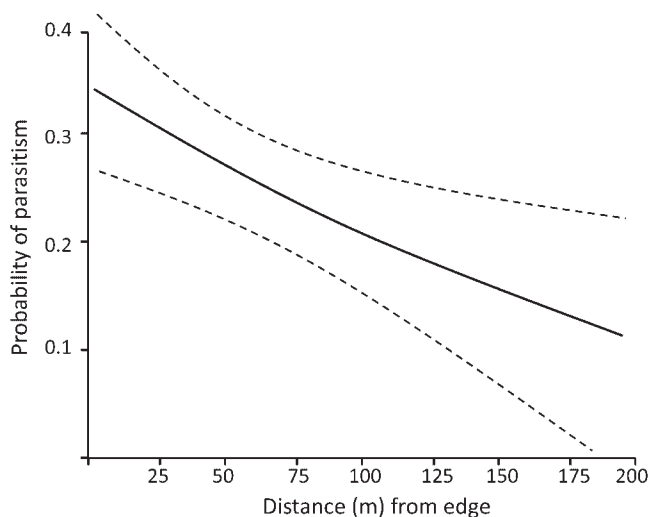


Figure 3. Estimated probability and 95% confidence intervals of cowbird parasitism on southwestern willow flycatcher nests as a function of distance to habitat edge based on 6 sites in Arizona and Nevada, USA, 2003–2007.

Year and ordinal date were implicated in parasitism models, consistent with previous studies that documented variation in parasitism rates across years (McLeod et al. 2008). However, although previous studies documented a reduction in parasitism through the breeding season in flycatchers (Sedgwick and Knopf 1988, Chapa-Vargas and Robinson 2007), we found that parasitism rates increased through time. For example, only 15% of nests initiated prior to 10 June were parasitized, compared to 30% of nests initiated after that date. Nest survival remained relatively constant across time for unparasitized nests, but generally decreased through the season during the laying and incubation periods for parasitized nests (Fig. 2). Flycatchers may double-brood and will renest if the initial nesting attempt fails, and nest abandonment followed by renesting has been documented as a response to cowbird parasitism (Sedgwick and Knopf 1988). Clutch size of re-nests tends to be smaller than for first nests (Holcomb 1972) and fledglings from later nests have lower survival to the following year (McLeod et al. 2008). As a result, the decrease in parasitized nest survival through time that we documented likely has a smaller demographic effect than if those losses had occurred earlier in the season.

Our finding that rates of nest predation were higher for parasitized compared to unparasitized nests was similar to that of several other studies (Dearborn 1999, McLaren and Sealy 2000, Ortega and Ortega 2003, Kosciuch and Sandercock 2008, Hannon et al. 2009) and could have arisen through 3 non-exclusive mechanisms. First, cowbird nestlings could increase nest predation by attracting predators through the increased volume of their own (Haskell 1994, Dearborn 1999) or host (Parker et al. 2002) begging calls or by increasing parental feeding visits (Dearborn et al. 1998, Hoover and Reetz 2006). Second, nest predators at our sites could find nests in ways similar to that of cowbirds (e.g., using similar visual and auditory cues). Third, parasitized nests could experience higher predation if cowbirds act as nest predators and do not avoid preying on nests containing cowbird young (Arcese et al. 1992, 1996; Smith and Arcese 1994). This may be most likely when female cowbirds have ranges that overlap and previously parasitized nests are more easily discovered (Arcese et al. 1996). Our results are consistent with all 3 hypotheses. If the presence of cowbird nestlings increased nest predation, then parasitized nests should have greater predation at the nestling stage. Nest survival for parasitized nests was lowest at the nestling stage in our study. However, nest survival rates for parasitized nests were also lower than unparasitized nests at the incubation stage, when cowbird nestling behavior would not be a factor. We did not identify nest predators at the nests used in the analyses presented here, however, subsequent video-recordings at flycatcher nests at a subset of our sites have identified primarily diurnal, visually-oriented egg predators including American crow (*Corvus brachyrhynchos*), yellow-breasted chat (*Icteria virens*), Bewick's wren (*Thryomanes bewickii*) and gray catbird (*Dumetella carolinensis*; T. Theimer, Northern Arizona University, unpublished data) that likely search for nests in ways similar to that of

cowbirds. Finally, cowbirds have been recorded as nestling predators in other studies (e.g. Granfors et al. 2001, Stake and Cimprich 2003, Hoover and Robinson 2007, Benson et al. 2010) and video recordings in 2009 and 2010 at our Mesquite site revealed cowbirds killing and removing nestlings at 3 flycatcher nests, 1 of which contained a cowbird nestling (T. Theimer, Northern Arizona University, unpublished data). No other nest predators were recorded at this site.

MANAGEMENT IMPLICATIONS

Given that likelihood of parasitism decreased by 50% for nests >100 m from an edge and by 75% for nests >200 m from an edge, and that parasitism was linked with higher nest predation, managing for larger patches and patch shapes that minimize the amount of edge habitat is one option to reduce the impact of cowbirds at sites along the lower Colorado River. However, current land use practices and ownership limit the number of occupied sites that could be increased in size. Cowbird control may be a useful short-term solution if cowbirds have been documented as nest predators and control efforts are monitored to determine whether they result in increased productivity (Rothstein et al. 2003, Rothstein and Peer 2005). Given that we did not assess the demographic effects of cowbird control, however, the potential population-level benefits of cowbird control remain uncertain. Given that none of the habitat features we investigated were strongly associated with overall nest predation rates, identifying nest predators at individual sites may be the most effective means of developing management options for altering habitat to reduce predation by individual predator species (Benson et al. 2010).

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